# THE TIME OF EMBRYONIC DETERMINATION OF SENSORIA AND ANTENNAL COLOR AND THEIR RELATION TO THE DETERMINATION OF WINGS, OCELLI, AND WING MUSCLE IN APHIDS [1]

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In a general analysis of the applicability of the time-of-determination theory to intermediate aphids by Stiles (1938), nothing was said regarding the color of antennae and number of sensoria except to include them in the same tables with the wing, ocellar, and wing muscle development. The purpose of this paper is to report a study of the time of embryonic segregation of the sensoria and antennal color in the aphids previously reported (Stiles, 1938).

Shull, in investigations of gamic-parthenogenetic (1933) and winged-wingless (1937) intermediate aphids, did not include individuals whose intermediacy consisted in the color of their antennae because of the apparently erratic variability of that color. Nevertheless, antennal color and sensoria number are both characters very definitely related to the winged condition of aphids, hence should receive consideration in a study of forms intermediate between winged and wingless. Because most of the intermediates of this study did not express any intermediacy in their antennae, it was difficult to relate closely the intermediacy of this organ with that of the wings, ocelli and wing muscle. No closely graded series of antennal color or sensoria number could be found; therefore, it became apparent that these characters were probably of less value for this type of investigation than the wings, ocelli and wing muscle. It is for this reason that the records are somewhat incomplete regarding the nature of the antennae in the data presented (Stiles, 1938). However, enough antennae were studied to make possible an analysis of their relation to the general problem of intermediacy.

In my previous paper the antennae of the typical wingless aphid with respect to color are rated 0 (light) and that of the winged as 4 (dark), with intermediates represented by numbers between these. While 4 to 6 sensoria in the third segment of the antenna are typical

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in the wingless (Fig. 1 *A*) and about 15–18 in the winged aphids (Fig. 1 *B*), it is not considered safe, due to variation, to judge less than 10 sensoria as representing certain intermediacy in an antenna, although there are doubtless some with less that should be so considered.

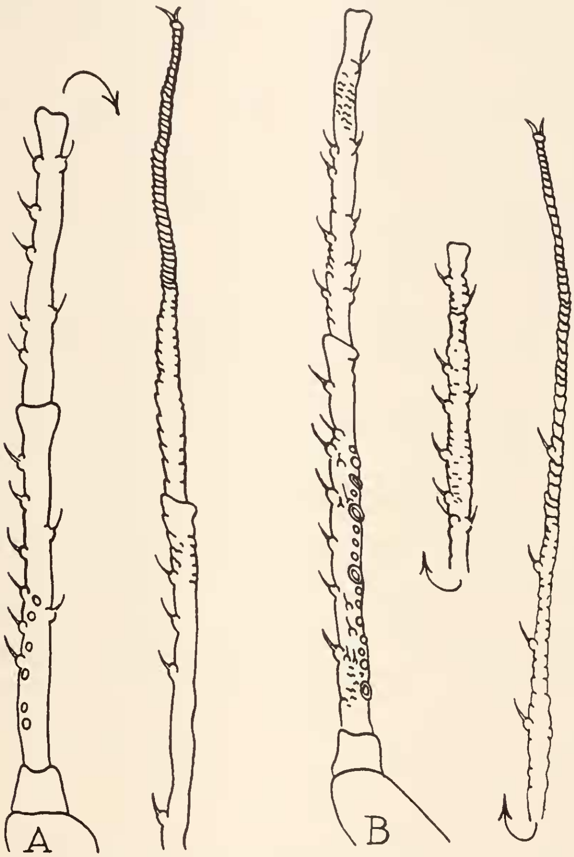


FIG. 1. Antennae of *Macrosiphum solanifolii* showing the difference in number of sensoria in typical wingless and winged forms. Sensoria are represented by the small circles on segment III. *A*, Wingless parthenogenetic female. *B*, Winged parthenogenetic female.

The data presented in Tables [2] I to IX inclusive (Stiles, 1938) show that the color of antennae and sensoria number are closely related; that is, in general a darkening of antennae is accompanied by an increase in sensoria number. The author is inclined to believe that, in a case

[2] To save republication of tables, all tables cited in this paper refer to a previous paper (Stiles, 1938).

where a slight darkening of the antennae may have been recorded with no corresponding increase in the number of sensoria, an error has been made in judging antennal color. Unless the color difference is marked, it is difficult to be sure of the antennal color. Nevertheless, records of both antennal color and sensoria number are useful inasmuch as one provides a check on the other. Since there has been found to be a close correlation between the number of sensoria and antennal color, with the number of sensoria a more reliable guide to antennal intermediacy than the color of antennae, henceforth these structures will be indicated by statements concerning only the sensoria.

With few exceptions, the data showed a correlation between the sensoria and the character of the wing muscle. An intermediate condition of sensoria, indicated by an increase in number as compared with wingless, was, in almost every such intermediate studied, associated with non-degenerate wing muscles. The one most notable exception is a case in which there is so little degeneration of muscle that degeneracy may be questioned.

Another correlation is apparent between intermediate sensoria and quantity of muscle, for in general increased sensoria are associated with a relatively large amount of wing muscle. An intermediate of particular interest in this connection is one in Table VI, slide 1061 *e* (1), wing .5, ocellar development .94, and wing muscle development .99 with 14 and 15 sensoria, which is almost normal for the winged. It has been difficult to relate the time-of-determination theory to the number of sensoria. On the basis of this theory, if sensoria were determined very late, as might be suspected from their correlation with wing muscle, one would expect more sensoria than is characteristic of typical wingless individuals in at least some of the intermediates with only .01 wing development which presumably changed to the winged condition very late in their embryogeny. This condition is not met in any of the intermediates with .01 wing development, yet there are many of these.

The data on intermediates, if the order of determination is wings, ocelli, and wing muscle as proposed by Stiles (1938), permit the interpretation that the greater number of sensoria characteristic of the winged aphid is determined neither very late nor early, but somewhere between these extremes. Increased sensoria cannot be determined early in development or they would be found more generally in intermediates with degenerate wing muscle; neither does it seem probable that they are determined very late or some of the aphids with a low degree of intermediacy (little development of wings) and non-degenerate muscles would possess intermediate antennae. With the exception of one, the most muscle found in intermediates with degenerate wing muscle is .57

of normal development, indicating a change to wingless before the late stages in the segregation of this organ. The one exception of much muscle associated with degeneracy is P–27 of Table V. Unfortunately the sensoria number and antennal color of this aphid are not known as it was selected for a typical winged aphid and it was only after a histological study that intermediacy was recognized. If the antennae had been the light color of wingless aphids, it would seem as though that feature would have been observed, although it could have been overlooked for they were not examined with a microscope. Of those aphids in this investigation which were rated as to antennal characters and in which there were degenerate wing muscles, it may be postulated that development in the direction of wings was not far enough advanced before a change to wingless occurred for increased sensoria to be determined. All aphids in which the non-degenerate muscles are correlated with a low degree of wing development and a small amount of wing muscle are individuals in which the change to wings came too late in their embryonic development for an increase in sensoria to be determined. Only intermediate-winged aphids which change from a wingless to a winged condition early enough in their embryogeny to have wing muscles comparatively well developed pass through that part of the developmental period in which an increased number of sensoria is determined. This hypothesis may be illustrated by using a horizontal line to represent the entire embryogeny with vertical lines intersecting at various points to set off periods of time, as below.

Embryonic order of determination—wings, ocelli, wing muscle.

Aphid begins embryogeny wingless and changes to winged.

*A*. Beginning of embryogeny | 1 | 2 | End of embryogeny

Period of sensoria determination

Aphid begins embryogeny winged and changes to wingless.

*B*. Beginning of embryogeny | 1 | 2 | End of embryogeny

Period of sensoria determination

In *A,* intermediates with a small amount of wing muscle change to the winged condition at a time later than the interval marked off by the perpendicular line number 2, and therefore do not possess more sensoria than the typical wingless aphids. In *B,* intermediates with degenerate muscles as a consequence of a winged-to-wingless transition, change to wingless before the time interval designated by 1 has been reached, and therefore do not possess an increased number of sensoria. Of the aphids in this study only those which changed from wingless to winged early enough to have considerable wing muscle passed through that part of the developmental period between the intervals 1 and 2.

These studies have led to the inference that the wings, ocelli, and wing muscles have their determination spread over considerable time, whereas the determination of the sensoria takes place in a relatively short time. An extensive series of intergradations in the development of the wings, ocelli, and wing muscles as contrasted with the decidedly limited series of the sensoria suggests this. From this analysis one concludes that increased sensoria are not determined until after the initial determination of wings, ocelli, and wing muscles; the former, however, complete their segregation before the latter.

From the data, it is concluded that the reason why aphids of this study with degenerate wing muscles did not usually possess increased sensoria is because the development in the direction of wings stopped short of the time when a greater number of sensoria would have been determined. Intermediates with considerable non-degenerate wing muscle changed from the wingless to the winged condition early enough to include in their development the period over which increased sensoria were determined. This analysis does not involve the inference that sensoria develop as a response to wing muscle, for in many cases the data show considerable wing muscle development without an intermediate number of sensoria. However, it is assumed that the time when increased sensoria in the embryogeny of the winged aphid are determined is indicated by the quantity of wing muscle. With the knowledge of the time when wing muscle is segregated in embryonic development as a point of reference, the time when sensoria characteristic of the winged aphid are determined can be ascertained provided that differentiation of the sensoria follows determination closely. According to this analysis, sensoria typical for winged forms are determined after wings, ocelli, and wing muscles.

## Summary

Dark antennal color and increased sensoria of winged aphids are considered to be characters closely correlated in development, for in general when there was a darkening of antennae there was a corresponding increase in the number of sensoria. In practically all cases increased sensoria were correlated with a relatively large amount of non-degenerate wing muscle. It is concluded that embryonic determination of dark antennal color and increased sensoria takes place in a comparatively

short period of time as compared with that of wings, ocelli, and wing muscle. The data make it seem probable that dark antennal color and extra sensoria, characteristic of the winged aphid, are determined after the wings, ocelli, and wing muscle; the former, however, complete their segregation before the latter.

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